

## Increase of arachnid abundance and biomass at water shores

Johannes HENSCHHEL, Helmut STUMPF & Dieter MAHSBERG

Theodor-Boveri-Institut für Biowissenschaften der Universität, Zoologie III,  
Am Hubland, D-97074 Würzburg, Germany.

**Increase of arachnid abundance and biomass at water shores.** - Arthropod communities were studied in the herb layer (*Urtica dioica*) along nine freshwater shores in southern Germany to ascertain how community structure changes with distance from the water. Spider abundance and biomass tended to be higher within 2 m of the shores than at comparable terrestrial sites located 30–50 m distant from the shores. This distribution of spiders may be correlated with the distribution of flying imagoes of aquatic insects. Besides these quantitative differences, the spider species assemblages were broadly similar at the shores compared to distant sites. By contrast, other predators appeared to be less abundant at the shore sites compared to distant sites. No consistent trends were, however, evident for herbivores. We nevertheless suggest that abundant polyphagous spiders have the potential to depress terrestrial prey populations at the shore and describe how we are testing this.

**Key-words:** abundance – biomass – trophic interactions – community ecology – subsidy.

### INTRODUCTION

Two disparate habitats abut at water shores. This is thus a convenient place to examine the relationship of spiders with very different sources of prey (POLIS & HURD 1995a). Water shores are often prey-rich areas at which spiders concentrate in high densities (GREENSTONE 1978; JADRANKA 1992; POLIS & HURD 1995a, b) within the limitations of competition, territoriality and cannibalism (RIECHERT 1976; KRONK & RIECHERT 1979; GILLESPIE 1981; JANETOS 1982; MORSE & FRITZ 1982; WISE 1993).

In a preliminary examination of the question of whether the arthropod predator-prey ratios differ at freshwater shorelines compared to sites of similar structure situated away from these shores, we studied arthropod communities at nine sites in Bavaria. To investigate communities in the vegetative layer as a function of distance from the shore, one needs to control for structural habitat variables that may influence

densities independent of location (e.g., GUNNARSON 1990). These structural variables are particularly the type, density and height of the vegetation and the degree of shelter from wind and sun provided by surrounding structures.

The greater stinging nettle *Urtica dioica* L. served as our focal plant community to standardize habitat structure and sampling procedure. The insects associated with nettles tend to form a characteristic community (DAVIS 1983) that facilitates identification and analyses. The characteristic spatial and structural arrangement of nettles may likewise facilitate the development of a characteristic arachnid community.

Our analyses lead us to suggest definitive tests of the effects that allochthonous processes have on trophic interactions occurring at the interfaces of major habitat types such as water shores.

## METHODS

During July–August 1995, nine localities in Bavaria were visited, of which five were along rivers (Sites 1–5 along the Main river at Würzburg, Heidingsfeld, Münsterschwarzach, and Dettelbach and along the Amper river at Palzing, respectively) and four were along tributary streams of the Main (Sites 6–9 along the Eheriedbach at Kaltensondheim and Kitzingen, the Zeubelriedbach at Erlach, and the Kürnachbach at Lengfeld, respectively).

At each locality, two undisturbed sites with nettles were selected, one < 2 m from the water shore, the other 30–50 m away. The two sites were comparable in terms of exposure to sun and wind, and the height, density and patch size of nettles. In a 1-m<sup>2</sup> area at each site, nettles were beaten for 1 min with a stick over a beating tray of 86 cm diameter: the approximate volume sampled was 1 m<sup>3</sup> of nettles. Arthropods were captured with an electric vacuum pump (HENSCHEL 1995) and preserved in 75% ethanol.

Arthropods were identified and counted and their body lengths were measured under a stereomicroscope, excluding projections at both ends. Dry mass (mg) of arthropods was estimated by using the general equations of HENSCHEL *et al.* (1996) for spiders and harvestmen and of ROGERS *et al.* (1976) for insects. Arthropods were identified to the lowest taxonomic level at which distinctions were discernable, hereafter termed taxonomic units. Where possible, spiders were identified to species (following PLATEN *et al.* 1995), or, if immature, to genus or family; very small juveniles were not identified beyond order. Terrestrial insects were classified to family level and taxonomic units; where immatures could not be matched with imagoes, they were registered separately (e.g., Cicadellidae). The number of taxa may be overestimated for insects and underestimated for spiders.

The sample populations were divided into three major categories, namely, spiders, other arthropod predators and resident terrestrial herbivorous insects. The other arthropod predator category comprised harvestmen, pseudoscorpions, nabid bugs and carabid, coccinellid, and staphylinid beetles. The herbivorous insect category included only those taxa and sizes of Homoptera, Heteroptera, and Coleoptera that resided on

netles and were known or expected to be captured by the predators (pers.obs. of > 500 predation events). Resident terrestrial invertebrates that were excluded were snails, isopods, ants, Dermaptera, Collembola, Lepidoptera, Thysanoptera and Acari that were not adequately covered by our sampling method or were of peripheral interest. Excluded taxa comprised 28% of all sampled individuals.

## RESULTS

Of the 2323 arthropods analyzed, spiders represented 39.99%, harvestmen 1.64% and other predators 4.61%. We collected 36 spider taxa of which up to 14 occurred in one sample (Fig. 1).

Spider abundance, biomass, and number of taxa were usually highest at the shore (Fig. 1, 2a & 3), significantly so for absolute biomass and number of taxa (Wilcoxon signed rank test  $T \leq 4$ ;  $n = 9$  pairs;  $P < 0.05$ ) and the proportion of abundance and biomass in each sample ( $T \leq 5$ ;  $n = 9$  pairs;  $P < 0.05$ ). A notable exception was Site 3, where extraordinarily many *Gongylidium rufipes* ( $n = 107$ ) were collected 30 m from the shore (Fig. 2a). Overall, 60% of the individuals and 71% of the biomass of spiders were collected at the shore sites.

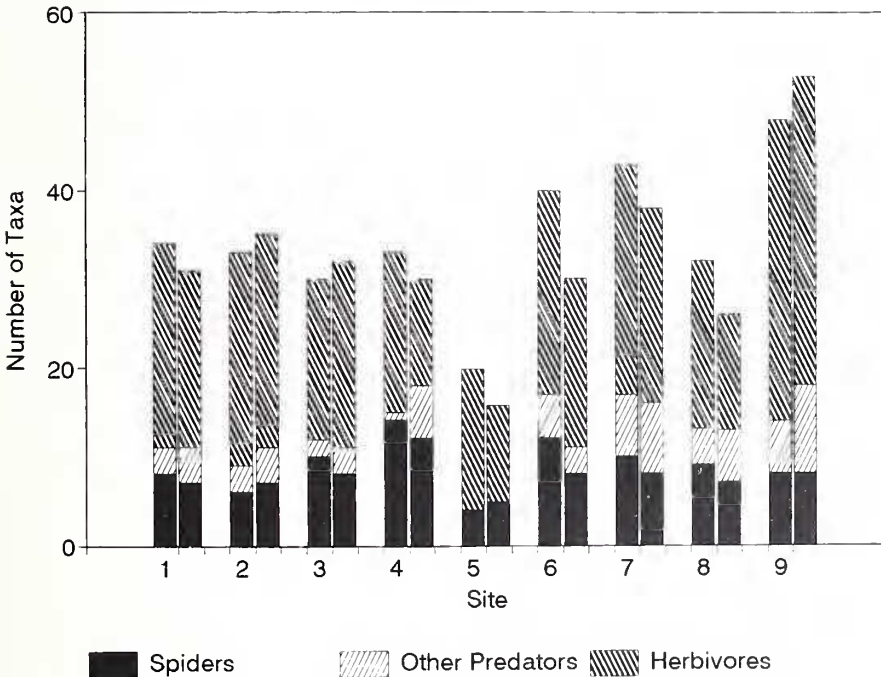


FIG. 1

Number of taxa of spiders, other predators and terrestrial herbivorous insects at nine river and stream shores (left bar) compared to matched sites > 30 m distant (right bar).

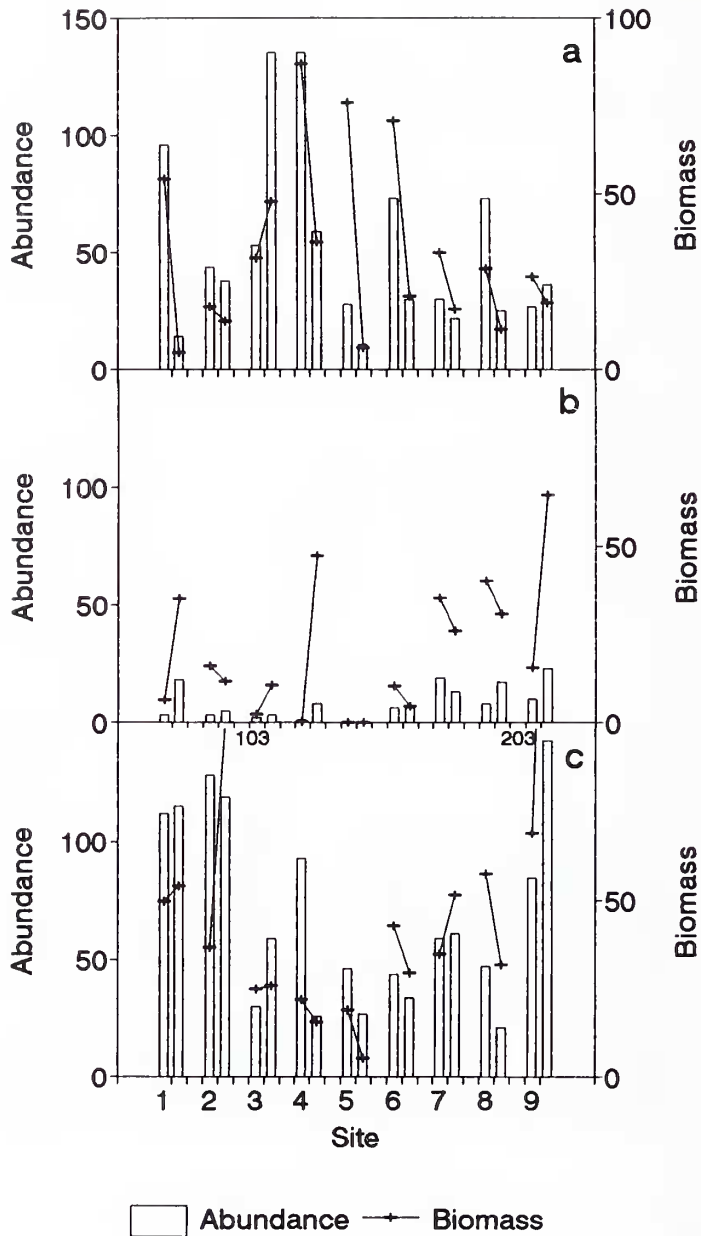


FIG. 2

Abundance (bars) and biomass (crosses and lines) of (a) spiders, (b) other predators, and (c) herbivores at nine river and stream shores (left) compared to matched sites > 30 m distant (right).

Different species of spiders may respond differently to the proximity of the shore (Appendix A). The most common spider, *G. rufipes*, did not differ significantly between sites at and away from the shore ( $T = 14$ ;  $n = 9$  pairs;  $P > 0.05$ ). The next most common spiders, *Tetragnatha* sp. and *Clubiona* sp., however, tended to be hydrophilic ( $T \leq 4.5$ ;  $n = 9$  pairs;  $P < 0.05$ ). Other common species that were more numerous at the shores were *Singa hamata*, *Dictyna* sp. and *Metellina segmentata* (Appendix A). The only common species that were more numerous away from the shore were *Philodromus* sp. and *Linyphia hortensis*. Leaving aside 11 singletons, 64% of the taxa occurred both at the shore and  $> 30$  m distant (Appendix A); the other nine taxa were uncommon (total  $\leq 5$ ) and could have been missed at either the shore or distant sites. There is thus no evidence that there were differences in the species assemblage at the shore compared to  $> 30$  m distant.

The abundance and number of taxa of other predators tended to increase away from the shore (Fig. 1 & 2b;  $T \leq 5.5$ ;  $n = 9$ ;  $P < 0.05$ ), but the biomass was not significantly different. This pattern appeared to differ from that of the spiders, but the negative correlation was not significant ( $R_s = -0.31$ ;  $P = 0.20$ ). The absence of nabids and harvestmen at some localities reduced sample size so that we could not test differences for these taxa separately. The total number of nabids and harvestmen was higher away from the shore (Appendix B).

The abundance and biomass of herbivores did not present clear distribution trends with distance from the shore (Fig. 2c;  $T > 18$ ) nor relative to the abundance and

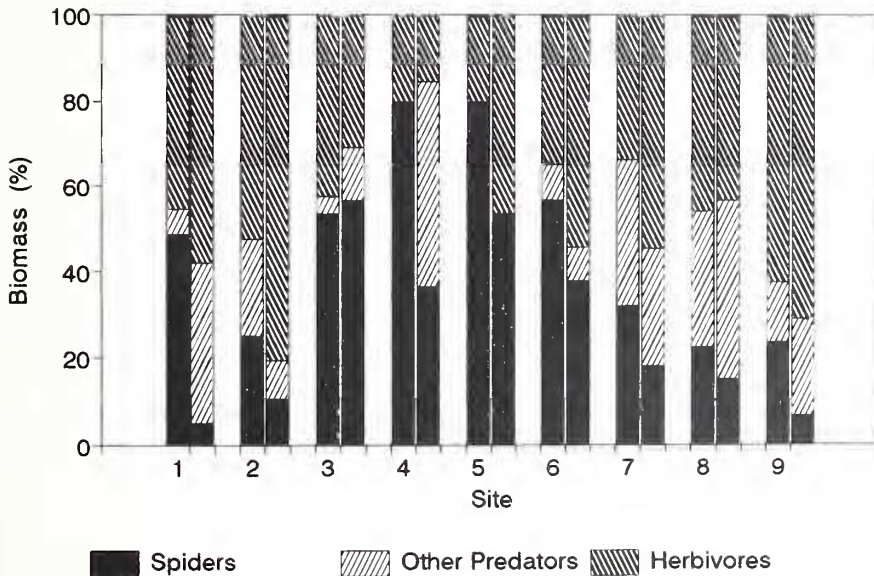


FIG. 3

Percent of the biomass represented by spiders, other predators and herbivores in each sample at nine river and stream shores (left) compared to matched sites  $> 30$  m distant (right).



biomass of spiders and other predators (Fig. 3;  $R_s = 0.14$ ;  $P = 0.58$ ). The number of taxa was higher at the shore (Fig. 1;  $T = 3.5$ ;  $n = 8$  pairs;  $P < 0.05$ ). Of the four most common families, Cicadellidae, Miridae, Anthocoridae, and Lygaeidae, only the Lygaeidae differed significantly with distance from the shore; they were less numerous at the shore ( $T = 2$ ;  $n = 7$  pairs;  $P < 0.05$ ).

## DISCUSSION

The abundance and biomass of spiders tended to be higher at water shores than at sites some distance away. Casual observations indicated that another major change as one approached a water shore was the increasing abundance of imagoes of aquatic insects, such as mosquitoes and midges, that are often captured by spiders. It is thus not surprising that spiders are abundant at shores, as spiders concentrate at prey-rich places (KAJAK 1965, 1978; RIECHERT & LOCKLEY 1984; NYFFELER & BENZ 1987; RIECHERT & BISHOP 1990; WISE 1993). Polyphagy is a key factor that provides spiders the capability to control populations of minor prey. If shore spiders are dependent on abundant prey of aquatic origin (GREENSTONE 1978), they may be decoupled from the less abundant prey of terrestrial origin. High densities of spiders at the shore may thus depress terrestrial prey populations; this effect declines with distance from the shore, as the abundance of aquatic imagoes declines. This effect may be a characteristic of interfaces of habitats that differ in richness and other qualities (PROVENCHER & RIECHERT 1994).

Apparent competition occurs where bottom-up effects increase top-down effects on different species, such as in the case of non-resident prey populations influencing resident prey via their common predators (HOLT 1984; HOLT & LAWTON 1993). The subsidy effect is one form of apparent competition that involves the allochthonous flow of food from one habitat (donor) to another (recipient), thus enriching the consumers in the recipient habitat, while the food source remains beyond recipient control (POLIS *et al.* 1995; POLIS & HURD 1995*a, b, c*; BUSTAMANTE *et al.* 1995). Long-term subsidies become reliable resources that increase the productivity of consumer populations. High densities of subsidized consumers are independent of their *in situ* resources, which they can depress without incurring negative feedback. In our case, aquatic insect imagoes subsidize shore spiders, that, in turn, can depress terrestrial insects.

In the present study, some of the predators other than spiders may be less abundant at the shore. This pattern may be explained by intraguild predation or competition (WISE 1993) or by the predators' response to the increasing abundance of terrestrial prey away from the shore where spiders do not depress the prey. Some of the non-spider predators are specialists and dependent on terrestrial insects, thus reducing their capability to depress such prey populations.

The suggestion of population control of terrestrial insects by polyphagous spiders needs to be tested in greater depth. The present preliminary investigation does not provide strong evidence that shore spiders depress terrestrial insects. Few samples and short distances of 30–50 m do not allow for good resolution; greater distances are difficult to find in Central Europe where microhabitats change between patchy

APPENDIX A: Development stage (J = Juvenile, A = Adult) and abundance of spider species captured at nine Bavarian localities at the shores and &gt; 30 m distant from the shores.

Species	Stage	Total		Shore		Distant	
		n	%	n	%	n	%
<b>Anyphaenidae</b>							
<i>Anyphaena accentuata</i> (Walck.)	J	3	(0.3)	3	(100)		(0)
<b>Aranaeidae</b>							
<i>Araniella</i> sp.	J	1	(0.1)	1	(100)		(0)
<i>Larinioides cornutus</i> (Cl.)	J	9	(1.0)	5	(55.6)	4	(44.4)
<i>Singa hamata</i> (Cl.)	A	1	(0.1)	1	(100)		(0)
<i>Singa</i> sp.	J	18	(1.9)	17	(94.4)	1	(5.6)
Araneida	J	8	(0.9)	1	(12.5)	7	(87.5)
<b>Clubionidae</b>							
<i>Cheiracanthium</i> sp.	J	3	(0.3)	3	(100)		(0)
<i>Clubiona lutescens</i> Westr.	A	5	(0.5)	5	(100)		(0)
<i>Clubiona stagnatilis</i> Kulcz.	A	1	(0.1)		(0)	1	(100)
<i>Clubiona</i> sp.	J	140	(15.1)	107	(76.4)	33	(23.6)
<b>Dictynidae</b>							
<i>Dictyna uncinata</i> Thorell	A	4	(0.4)	2	(50.0)	2	(50.0)
<i>Dictyna</i> sp.	J	20	(2.2)	16	(80.0)	4	(20.0)
<b>Linyphiidae</b>							
<i>Gongylidium rufipes</i> (L.)	A	6	(0.6)	5	(83.3)	1	(16.7)
<i>Gongylidium rufipes</i>	J	258	(27.8)	113	(43.8)	145	(56.2)
<i>Hypomma cornutum</i> (Blackw.)	A	1	(0.1)		(0)	1	(100)
<i>Linyphia hortensis</i> Sund.	J	26	(2.8)	7	(26.9)	19	(73.1)
<i>Linyphia triangularis</i> (CL.)	J	5	(0.5)	3	(60.0)	2	(40.0)
<i>Neriere montana</i> (CL.)	J	2	(0.2)	2	(100)		(0)
<i>Neriere</i> sp.	J	7	(0.8)	2	(28.6)	5	(71.4)
Linyphiidae	J	76	(8.2)	32	(42.1)	44	(57.9)
<b>Philodromidae</b>							
<i>Philodromus cespitum</i> (Walck.)	A	1	(0.1)		(0)	1	(100)
<i>Philodromus</i> sp.	J	27	(2.9)	8	(29.6)	19	(70.4)
<b>Salticidae</b>							
<i>Heliophanus auratus</i> C.L. Koch	A	1	(0.1)	1	(100)		(0)
<i>Heliophanus flavipes</i> Hahn	A	3	(0.3)		(0)	3	(100)
<i>Sitticus</i> sp.	J	1	(0.1)	1	(100)		(0)
<b>Tetragnathidae</b>							
<i>Metellina segmentata</i> (Cl.)	J	35	(3.8)	23	(65.7)	12	(34.3)
<i>Pachygnatha</i> sp.	J	1	(0.1)		(0)	1	(100)
<i>Tetragnatha montana</i> Simon	A	3	(0.3)	3	(100)		(0)
<i>Tetragnatha</i> sp.	J	170	(18.3)	137	(80.6)	33	(19.4)
<b>Theridiidae</b>							
<i>Achaearanea simulans</i> (Thorell)	A	1	(0.1)	1	(100)		(0)
<i>Enoplognatha ovata</i> (Cl.)	A	7	(0.8)	4	(57.1)	3	(42.9)
<i>Theridion varians</i> Hahn	A	2	(0.2)	2	(100)		(0)
Theridiidae	J	3	(0.3)	3	(100)		(0)
<b>Thomisidae</b>							
<i>Misumenops tripunctatus</i> (Fabr.)	J	1	(0.1)		(0)	1	(100)
<i>Ozyptila</i> sp.	J	1	(0.1)		(0)	1	(100)
<i>Xysticus</i> sp.	J	2	(0.2)		(0)	2	(100)
Thomisidae	J	13	(1.4)	5	(38.5)	8	(61.5)
Non det.	J	63	(6.8)	46	(73.0)	17	(27.0)
Total Number		929		559	(60.2)	370	(39.8)
Total Biomass (mg)		603		462	(70.7)	177	(29.3)

APPENDIX B: Number of taxa (NT) and abundance of families or species of predators other than spiders and of herbivores captured at our nine localities at the shore and &gt; 30 m distant from the shore

Family/Species	NT	Total n (%)	Shore n (%)	Distant n (%)
<b>OTHER PREDATORS</b>				
Heteroptera				
Nabidae	3	34 (23.4)	7 (20.6)	27 (79.4)
Coleoptera				
Carabidae	2	19 (13.1)	17 (89.5)	2 (10.5)
Coccinellidae	4	18 (12.4)	6 (33.3)	12 (66.7)
Staphylinidae	3	23 (15.9)	10 (43.5)	13 (56.5)
Neuroptera				
Chrysopidae	1	5 (3.4)	3 (60.0)	2 (40.0)
Pseudoscorpiones				
non det.	1	8 (5.5)	1 (12.5)	7 (87.5)
Opiliones				
<i>Oligolophus tridens</i> (C.L. Koch)	1	22 (15.2)	1 (4.5)	21 (95.5)
<i>Opilio canestrinii</i> (Thorell)	1	11 (7.6)	3 (27.3)	8 (72.7)
<i>Leiobunum rotundum</i> (Latr.)	1	2 (1.4)	2 (100.0)	0 (0.0)
non det.	1	3 (2.1)	2 (66.7)	1 (33.3)
Total Predators	18	145	51 (35.2)	94 (64.8)
Biomass		357	127 (35.4)	231 (64.6)
<b>HERBIVORES</b>				
Homoptera				
Cicadellidae	15	469 (37.6)	294 (62.7)	175 (37.3)
Psyllidae	1	75 (6.0)	48 (64.0)	27 (36.0)
Aphididae	2	17 (1.4)	9 (52.9)	8 (47.1)
Aphrophoridae	2	4 (0.3)	1 (25.0)	3 (75.0)
Delphacidae	1	2 (0.2)	0 (0.0)	2 (100.0)
Heteroptera				
Miridae	10	206 (16.5)	105 (51.0)	101 (49.0)
Anthocoridae	2	160 (12.8)	105 (65.6)	55 (34.4)
Lygaeidae	2	138 (11.0)	17 (12.3)	121 (87.7)
Pentatomidae	2	25 (2.0)	8 (32.0)	17 (68.0)
Loriculidae	1	1 (0.1)	1 (100.0)	0 (0.0)
Coleoptera				
Chrysomelidae	4	40 (3.2)	21 (52.5)	19 (47.5)
Apionidae	3	30 (2.4)	7 (23.3)	23 (76.7)
Curculionidae	2	27 (2.2)	10 (37.0)	17 (63.0)
Lathridiidae	1	25 (2.0)	7 (28.0)	18 (72.0)
Nitidulidae	3	21 (1.7)	11 (52.4)	10 (47.6)
Lagriidae	1	5 (0.4)	0 (0.0)	5 (100.0)
Anthicidae	1	4 (0.3)	0 (0.0)	4 (100.0)
Total Herbivores	53	1249	644 (51.6)	605 (48.4)
Biomass		877	357 (40.7)	520 (59.3)



landscapes, preventing standardized comparison. More detailed analyses of arthropods at replicate sites would provide a test of whether predators control herbivore populations at the shore. Another test is to examine the effect of spider removal on terrestrial insect populations. We are applying both approaches in ongoing studies.

#### ACKNOWLEDGEMENTS

We thank the Würzburger Versorgungs- und Verkehrs GmbH (WVV), the Government of Lower Frankonia and the Municipality of Würzburg for information and permission to carry out this study. JRH is a fellow of the Alexander-von-Humboldt-Foundation. Inge Henschel and Margit Enders assisted in the field, Norbert Schneider and Gerhard Vonend adapted apparatus. Ulmar Grafe commented on the manuscript.

#### REFERENCES

- BUSTAMANTE, R.H., BRANCH, G.M. & EEKHOUT, S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelp. *Ecology* 76: 2314–2329.
- DAVIS, B.N.K. 1983. Insects on nettles. *Cambridge University Press, Cambridge*, 65 pp.
- GILLESPIE, R.G. 1981. The quest for prey by the web building spider *Amaurobius similis* (Blackwell). *Animal Behaviour* 29: 953–954.
- GREENSTONE, M.H. 1978. The numerical response to prey availability of *Pardosa ramulosa* (McCook) (Araneae: Lycosidae) and its relationship to the role of spiders in the balance of nature. *Symposium of the zoological Society of London* 42: 183–193.
- GUNNARSSON B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *Journal of Animal Ecology* 59: 743–752.
- HENSCHEL, J.R. 1995. Ein handliches Vakuumsammelgerät für die Erfassung von Spinnen und Insekten (A handy vacuum collector for catching spiders and insects). *Arachnologische Mitteilungen* 9: 67–70.
- HENSCHEL, J.R., MAHSBERG, D. & STUMPF, H. 1996. Mass-length relationships of spiders and harvestmen (Araneae and Opiliones). *Revue suisse de Zoologie*, vol. hors-série: 265–268.
- HOLT, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124: 377–406.
- HOLT, R.D. & LAWTON, J.J. 1993. Apparent competition and enemy-free space in insect host-parasitoid communities. *American Naturalist* 142: 623–645.
- JADRANKA, M. 1992. Spinnenfauna in Uferbereichen: Artengemeinschaften und ihre räumliche Einnischung. *Diploma thesis, Ludwig-Maximilian-University of Munich, Munich*, 104 pp.
- JANETOS, A.C. 1982. Foraging tactics of two guilds of web-spinning spiders. *Behavioural Ecology and Sociobiology* 10: 19–27.
- KAJAK, A. 1965. An analysis of food relations between the spiders *Araneus cornutus* Clerck and *Araneus quadratus* Clerck and their prey in meadows. *Ekologia Polska, Seria A*, 32: 717–764.
- KAJAK, A. 1978. Invertebrate predator subsystem, pp. 539–589. In: Grasslands, systems analysis and man (BREYMEYER, A.J. & VAN DYNE, G.M. eds). *Cambridge University Press, Cambridge*.

- KRONK, A.W. & RIECHERT, S.E. 1979. Parameters affecting the habitat choice of *Lycosa santrita* Chamberlin and Ivie. *Journal of Arachnology* 7: 155–166.
- MORSE, D.H. & FRITZ, R.S. 1982. Experimental and observational studies of patch choice at different scales by the crab spider *Misumena vatia*. *Ecology* 63: 172–182.
- NYFFELER, M. & BENZ, G. 1987. Spiders in natural pest control: A review. *Journal of Applied Entomology* 103: 321–339.
- PLATEN, R., BLICK, T., BLISS, P., DROGLA, R., MALTEN, A., MARTENS, J., SACHER, P. & WUNDERLICH, J. 1995. Verzeichnis der Spinnentiere (excl. Acarida) Deutschlands (Arachnida: Araneida, Opilionida, Pseudoscorpionida). *Arachnologische Mitteilungen, Sonderband 1*: 1–55.
- POLIS, G.A., HOLT, R.D., MENGE, B.A. & WINEMILLER, K.O. 1995. Time, space, and life history: influences on food webs. In: *Food webs: integration of patterns and dynamics* (POLIS, G.A. & WINEMILLER, K.O. eds). *Chapman & Hall, New York*, pp. 435–460.
- POLIS, G.A. & HURD, S. 1995a. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences* 92: 4382–4386.
- POLIS, G.A. & HURD, S. 1995b. Allochthonous input across habitats, subsidized consumers and apparent trophic cascades: examples from the ocean-land interface, pp. 275–285. In: *Food Webs: Integration of Patterns and Dynamics* (POLIS, G.A. & WINEMILLER, K. eds). *Chapman & Hall*.
- POLIS, G.A. & HURD, S. 1995c. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist*, in press.
- PROVENCHER, L. & RIECHERT, S.E. 1994. Model and field test of prey control effects by spider assemblages. *Environmental Entomology* 23: 1–17.
- RIECHERT, S.E. 1976. Web-site selection in the desert spider *Agelenopsis aperta* (Gertsch). *Oikos* 27: 311–315.
- RIECHERT, S.E. & BISHOP, L. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology* 71: 1441–1450.
- RIECHERT, S.E. & LOCKLEY, T. 1984. Spiders as biological control agents. *Annual Review of Entomology* 29: 299–320.
- ROGERS, L.E., HINDS, W.T. & BUSCHBOM, R.L. 1976. A general weight vs. length relationship for insects. *Annals of the entomological Society of America* 69: 387–389.
- WISE, D.H. 1993. Spiders in ecological webs. *Cambridge University Press, Cambridge*, 328 pp.